The Jiyuan Tetrapod Fauna of the Upper Permian of China: New Pareiasaur Material and the Reestablishment of Honania complicidentata

Authors: Xu, Li, Li, Xing-Wen, Jia, Song-Hai, and Liu, Jun

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The Jiyuan Tetrapod Fauna of the Upper Permian of China: New pareiasaur material and the reestablishment of *Honania complicidentata*

LI XU, XING-WEN LI, SONG-HAI JIA, and JUN LIU

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Honania complicidentata and *Tsiyuania simplicidentata* are pareiasaur taxa based on material from the Shangshihezi Formation of Jiyuan, Henan Province, China that were earlier designated as nomina vana. Based on the study of new material, and the reexamination of old specimens, we determine that the pareiasaur material from Jiyuan represents a single species that differs from all known species from other localities. Thus, we resurrect the name *H. complicidentata* for the material from Jiyuan. *H. complicidentata* is characterized by maxillary teeth with high crowns, dentary teeth slightly posteriorly inclined compared to the dentary dorsal margin, nearly all preserved marginal teeth have a cusped cingulum on the lingual surface, and humerus without an ectepicondylar foramen. Phylogenetic analysis shows *Honania* is more basal than *Shansisaurus* and *Shihtienfenia* from the Sunjiagou Formation of China.

Key words: Reptilia, Pareiasauria, phylogeny, Permian, Shangshihezi Formation, China, Jiyuan.

Li Xu [xuli.312@163.com] and Song-Hai Jia [jiasonghai1962@qq.com], Henan Geological Museum, Zhenzhou, 450018, China.
Xing-Wen Li [didalixingwen@163.com] and Jun Liu [liujun@ivpp.ac.cn] (corresponding authors), Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, China.

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Introduction

Pareiasaurs are a group of herbivorous parareptiles that had a worldwide distribution during the Middle and Late Permian (Lee 1997a). In China, six pareiasaur species in six separate genera have been named (Li et al. 2008). Among them, four taxa were based on material collected from the Sunjiagou Formation of Shanxi Province, including *Shihtienfenia permica* from Baode County (Young and Yeh 1963), and *Shansisaurus xuecunensis*, *Huanghesaurus liulinensis*, and *Sanchuansaurus pygmaeus* from Xuecun Town, Liulin County (Cheng 1980; Gao 1983, 1989), while *Honania complicidentata* and *Tsiyuania simplicidentata* are from the Shangshihezi (Upper Shihhotse) Formation of Jiyuan, Henan Province (Young 1979). Lee (1997a) presented a comprehensive taxonomic revision of pareiasaurs, and recognized three valid species from China: *S. permica*, *S. xuecunensis*, and *S. pygmaeus*. He argued that the differences between *Honania* and *Tsiyuania* only reflected the differences between upper and lower jaw teeth, and referred all material from this locality to *Sanchuansaurus*. Lee considered the types alone to be indeterminate, and declared the two taxa nomina vana. Other authors also regarded *Honania* and *Tsiyuania* as questionable taxa (Sun et al. 1992; Li et al. 2008). Recently, *H. liulinensis* and *S. pygmaeus* were designated junior synonyms of *S. xuecunensis* (Li and Liu 2013).

In 2010, new material was collected by Henan Geological Museum, mostly pareiasaur bones comprising cranial and postcranial elements. They confirm the referred teeth of *H. complicidentata* are lower marginal teeth and those of *T. simplicidentata* are upper marginal teeth. After comparison with other pareiasaurs, we show that these specimens represent a single pareiasaur taxon that is different from all other species and that *H. complicidentata* is valid. The phylogentic analysis shows *Honania* is more basal than *Shansisaurus* and *Shihtienfenia*.

Institutional abbreviations.—HGM, Henan Geological Museum, Zhenzhou, Henan, China; IGCAGS, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

Geological setting

All studied specimens in this paper were collected from fossil locality 63024, the type locality and horizon of *Honania complicidentata* and *Tsiyuania simplicidentata*. These specimens were concentrated within a thin layer of dark purple fine sandstone that is approximately 30 cm thick. This horizon is referred to the upper part of the Shangshihezi Formation, which is overlaid by the Sunjiagou Formation. All collected bones are disarticulated, and most of them are incomplete.

Systematic palaeontology

Reptilia Laurenti, 1768

Parareptilia Olson, 1947

Pareiasauria Seeley, 1888

Genus *Honania* Young, 1979

Type species: *Honania complicidentata* Young, 1979; monotypic, see below.

Diagnosis.—As for the monotypic type species.

Honania complicidentata Young, 1979

Figs. 1–7.

1979 *Honania complicidentata* sp. nov.; Young 1979: 102, text-fig. 4.
1979 *Tsiyuania simplicidentata* sp. nov.; Young 1979: 103, text-fig. 5.
1979 *Taihangshania imperfacta* sp. nov.; Young 1979: 104, text-figs. 6, 7, 8, 9.

Syntypes: IVPP V 4015.1 and 2, two isolated dentary teeth.

Type locality: Huakedaliang, Dayu Township, Jiyuan City, Henan Province, China.

Type horizon: Upper portion of Shangshihezi Formation, Permian.

Referred specimens.—IVPP V 4016, five maxillary teeth (formerly referred to *Tsiyuania simplicidentata*). IVPP V 4012.1, parietal; IVPP V 4012.2, prefrontal; IVPP V 4017.1, 3, 11, 36–52, teeth; 5, cervical vertebra; 6, ventral portion of ilium; 7, proximal portion of pubis; 8, posterodorsal portion of ilium; 9, proximal portion of ischium; 10, distal end of ischium; 18, distal end of right radius; 19, fragment of scapula; 20, distal end of left radius; 24, left splenial; 25, right splenial; 26, neural arch of dorsal vertebra; 27, caudal vertebra (all formerly *Taihangshania imperfacta* in Young 1979); IVPP V 4018.14, a broken tooth (formerly *Wangwusaurus tayuensis* in Young 1979: fig 12i); IVPP V 4019.2, a tiny tooth (formerly *Hwanghocynodon multienspidus* in Young 1979: fig. 13b). HGM 41HIII 0423, left maxilla; 24, left maxilla; 25, left dentary; 26, right dentary; 27, dorsal vertebra; 28, sacral vertebra with ribs; 29, sacral neural arch with ribs; 30, dorsal rib; 31, right scapula; 32, interclavicle; 33, left clavicle; 34, right ilium; 35, left humerus; 36, right humerus; 37, right ulna; 38, distal end of right radius; 39, right femur; 40, right tibia; 41, quadrate; 42; quadratojugal; 43, metacarpal or metatarsal.

Emended diagnosis.—This species has the following autapomorphies: maxillary teeth with high crown (height of exposed tooth crown greater than twice height of crown above the level of cingulum), dentary teeth slightly posteriorly inclined compared to dorsal margin of dentary, nearly all preserved marginal teeth have cusped cingulum on the lingual surface (this feature may also be present in *Arganaceras*), humerus without ectepicondylar foramen. It is also differentiated from *Shansisaurus* by lingual surface of dentary teeth smooth and featureless, maxillary teeth less closely spaced, maxillary boss moderately developed; from *Arganaceras* by ventrally directed maxillary teeth. It is differentiated from *Shitienfenia* by straight anterior margin of scapula blade near dorsal end and slightly convex iliac dorsal margin.

Description

The only identified cranial bones are the maxilla, prefrontal, parietal, quadrate, quadratojugal, dentary, and splenial. Most of the postcranial elements are preserved, but many bones underwent extensive compression and thus appear flattened; only the relatively complete bones are described here.

Four humeri from this locality show that there are at least three individuals in the collected pareiasaur bones. Two similar sized left clavicles indicate that at least two similar size individuals present. Thus, no two bones can be safely referred as same individual here.

Maxilla.—Specimen HGM 41HIII0423 is an incomplete left maxilla bearing six functional teeth and one newly erupted tooth (Fig. 1A). The preserved length is approximately 135 mm, and the estimated length of the upper jaw (premaxilla plus maxilla) would be ca. 160 mm. Most of the maxilla is preserved except for the partially broken posterior part.

The maxilla is slightly convex laterally and concave medially. Its lateral surface is rugose, but lacks distinct ornamentation. Its anterodorsal margin forms the posteroventral border of the external naris. Two foramina are located anteroposteriorly, and are open anteroventrally. They are very far apart, previously known only in the holotype of *Sanchuansaurus* (Gao 1989; Lee 1997b). Of these, the anterior one is the large, prominent anterior maxillary foramen (the anterior lateral maxillary foramen of Laurin and Reisz 1995). Both of them may be openings for the arteria alveolis superior (Jalil and Janvier 2005). Above the anterior maxillary foramen, a low boss is weakly developed. Posterior to the boss, the external surface is concave, forming the lateral maxillary depression, as in *Arganaceras* (Jalil and Janiver 2005). A horizontal palatal ledge extends anteroposteriorly, and its anterior end swells and curves slightly dorsally to the external naris. This ledge forms the anterolateral border of the internal naris.

Prefrontal.—Specimen IVPP V 4012.2 forms part of the orbit, and a rounded boss on its lateral margin. Its outer surface is sculptured with rugose ridges (Fig. 1B). It is hard to identify this bone; it is tentatively identified as the prefrontal, by comparison with the skull of *Pareiasuchus nasicorns* (Lee et al. 1997).

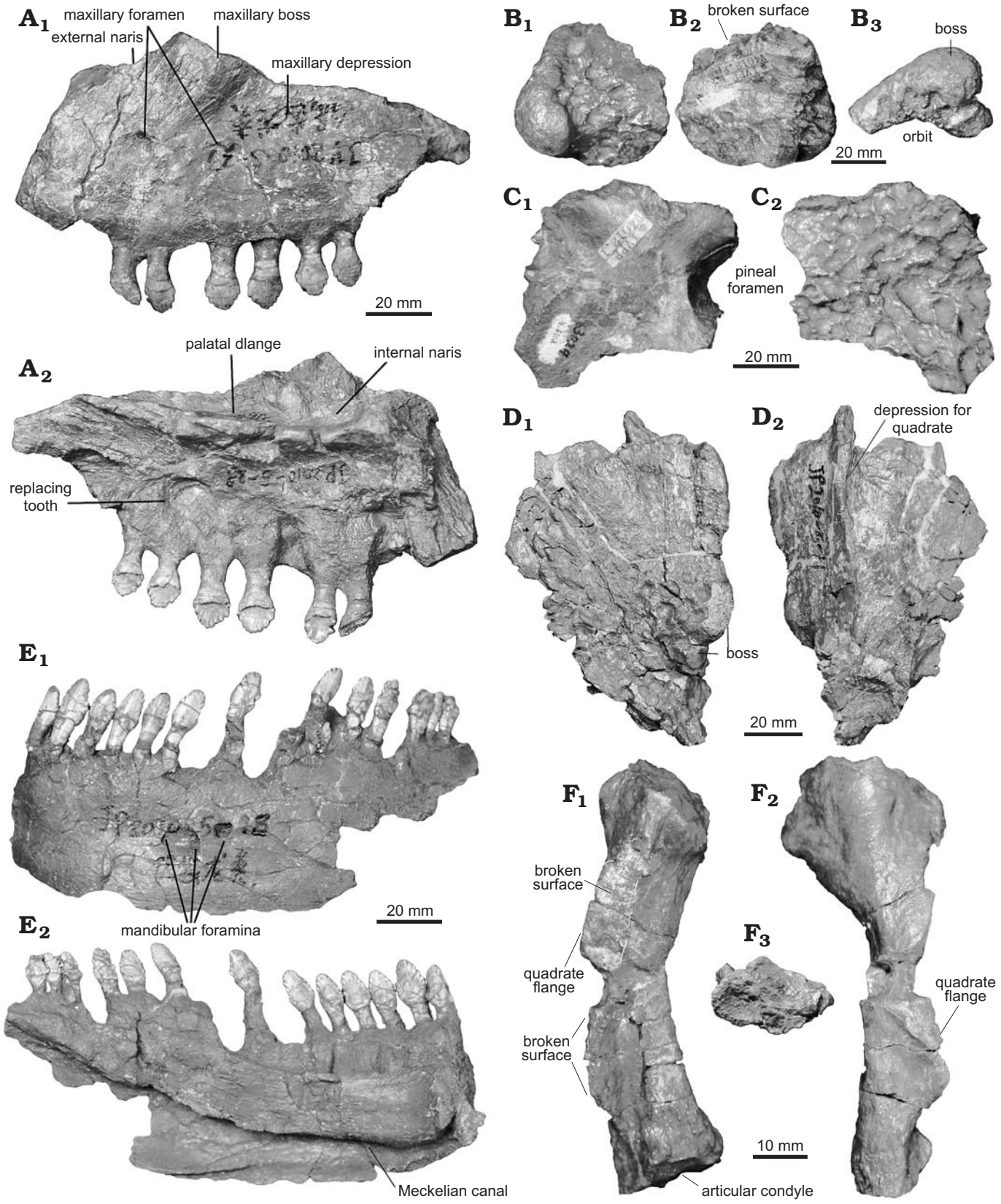


Fig. 1. Pareiasaur reptile *Honania complicidentata* Young, 1979 (Upper Permian, Shangshihezi Formation of Jiyuan, Henan Province, China). **A**. HGM 41HIII0423, left maxilla with teeth, in lateral (A_1) and medial (A_2) views. **B**. IVPP V4012.2, formerly referred to Labyrinthodontia (Young, 1979), ?prefrontal in dorsal (B_1), ventral (B_2), and lateral (B_3) views. **C**. IVPP V4012.1, formerly referred to Labyrinthodontia (Young, 1979), parietal in ventral (C_1) and dorsal (C_2) views. **D**. HGM 41HIII0442, incomplete left quadratojugal in lateral (D_1) and medial (D_2) views. **E**. HGM 41HIII0425, left dentary with teeth, in lateral (E_1) and medial (E_2) views. **F**. HGM 41HIII0441, incomplete left quadrate in anterior (F_1), posterior (F_2), and ventral (F_3) views.

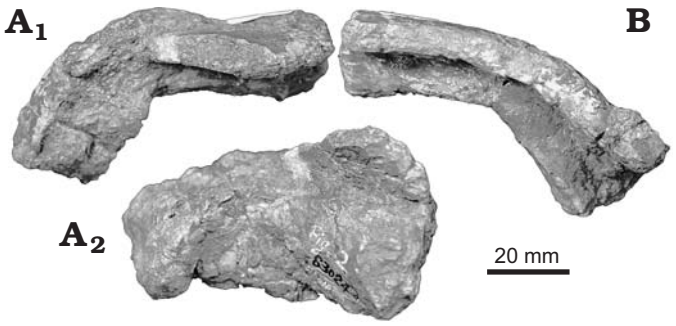


Fig. 2. Pareiasaur reptile *Honania complicidentata* Young, 1979 (Upper Permian, Shangshihezi Formation of Jiyuan, Henan Province, China). **A**. IVPP V 4017.24, the incomplete left splenial in dorsal (A_1) and posterior (A_2) views. **B**. IVPP V 4017.25, the incomplete right splenial in dorsal view.

Parietal.—Specimen IVPP V 4012.1 is heavily sculptured with irregular ridges. The round pineal foramen lies on the medial margin (Fig. 1C).

Quadratojugal.—Specimen HGM 41HIII0442 is identified as part of the left quadratojugal (Fig. 1D). Only the posterior portion is preserved. The bone is generally a thin plate, but its postoventral corner bears rounded pits and bosses and is thickened. The external surface of the upper portion is unornamented or bears a shallow furrow. A flange extends dorsoventrally from the inner surface to accommodate the quadrate.

Quadrate.—Specimen HGM 41HIII0441 (Fig. 1F) is identified as a left quadrate by comparison with the quadrate of *Arganaceras vacanti* (Jalil and Janvier 2005: fig. 21).

The rugose dorsal end, which contacts the paroccipital process, is much larger than the articular condyle, which is wider than long. The articular surface is roughly triangular in ventral view, and its anterior side turns dorsally. A shallow groove divides the surface into a larger medial part and smaller lateral parts. The medial flange to contact the pterygoid is not preserved.

Dentary.—Specimen HGM 41HIII0425 is a left dentary bearing 13 teeth (Fig. 1E), which is almost complete except for the ventroposterior portion. The preserved part measures 145 mm in length. Its anterior end bears a rugose articulating surface for the right dentary, and is the dentary symphysis. The bone curves laterally, and the lateral surface is relatively smooth without distinct ornamentation.

Three closely spaced foramina are visible on the lateral surface. The small anterior one faces posteriorly, the wide middle one opens anteriorly, and the large posterior one opens laterally and lies slightly dorsally. A shallow groove, possibly for blood vessels, connects the anterior and middle foramina, while the posterior foramen could be the foramen dentofaciale majus (Lee et al. 1997).

Lacking the splenial, the medial surface of the dentary is exposed. The dentary forms the dorsal wall of the Meckelian canal. The canal, which is partially occupied by the Meckel's cartilage, extends horizontally from the symphysis along the whole length of the bone.

Splenial.—Two incomplete splenials are identified: IVPP V 4017.24 is a left splenial and IVPP V 4017.25 a right one (Fig. 2). Both are anterior portions close to the symphysis. The bone is strongly curved, and the symphysial portion is swollen. On the dorsal side, a shallow middle groove and lateral flange serve to receive the dentary.

Dentition.—All maxillary teeth are deeply thecodont, and the replacement teeth lie medial to the functional teeth (Fig. 1A). The functional teeth are aligned in a single row, and they are not closely spaced, so the adjacent crowns do not overlap as in the holotype of *Sanchuansaurus* (Gao 1989). The preserved teeth are different in size; the last three teeth decrease remarkably in size posteriorly. Each tooth is slightly curved medially and expanded anteroposteriorly. The upper part of the crown is roughly triangular in medial view, with a convex labial surface and a concave lingual surface (Fig. 3). The majority of the preserved teeth have ten anteroposteriorly-arranged cusps on the tip of the crown, and a cusped cingulum on the base of the lingual surface of the crown. The middle three cusps are more closely spaced than anterior and posterior cusps (Fig. 3), just as in *Bradysaurus baini*, *Bradysaurus seeleyi*, *Nochelesaurus*, *Embrithosaurus* (Lee 1997b), and the holotype of *Sanchuansaurus* (Gao 1989; but not as Lee 1997b). These maxillary teeth are the same shape as the type teeth of *Tsiyuania simplicidentata*, which are broken (Fig. 3A). The maximum crown width is 6.5 mm in

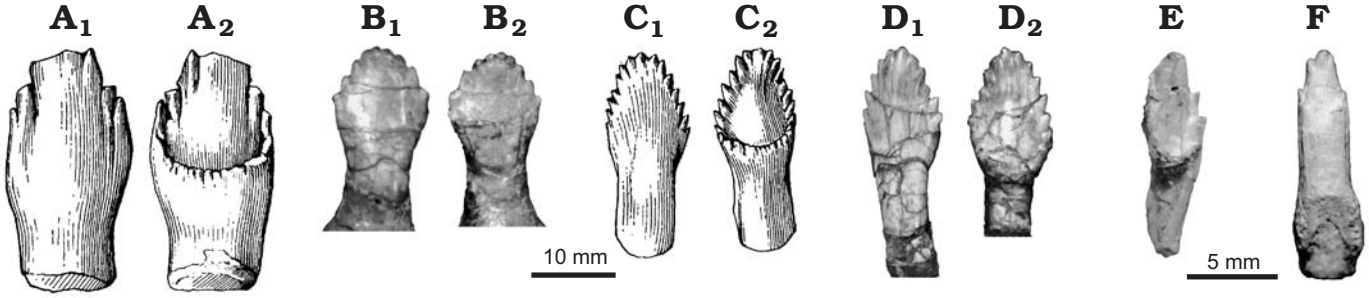


Fig. 3. Tooth of pareiasaur reptile *Honania complicidentata* Young, 1979 (Upper Permian, Shangshihezi Formation of Jiyuan, Henan Province, China); in labial (A_1–D_1, E, F) and lingual (A_2–D_2) views. **A**. IVPP V 4016.1, syntype of *Tsiyuania simplicidentata* (Young, 1979), maxillary tooth (from Young 1979: fig. 5). **B**. HGM 41HIII0423, maxillary tooth. **C**. IVPP V 4015.1, syntype of *Honania complicidentata* (Young, 1979), dentary tooth (from Young 1979: fig. 4). **D**. HGM 41HIII0424, dentary tooth. **E**. IVPP V 4018.14, former *Wangwusaurus tayuensis* (Young, 1979). **F**. IVPP V 4019.2, former *Hwanghocynodon multienspidus* (Young, 1979).

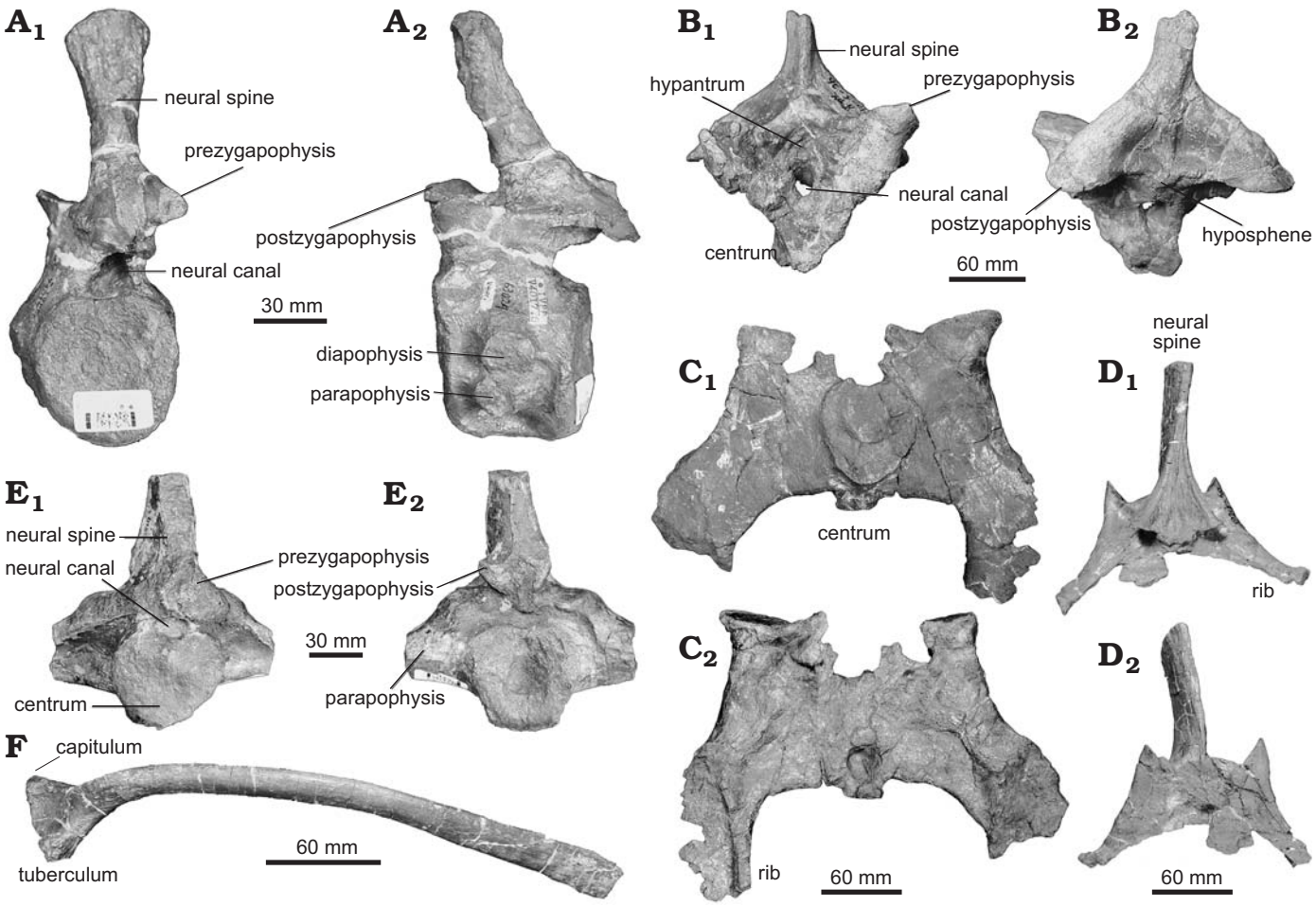


Fig. 4. Pareiasaur reptile *Honania complicidentata* Young, 1979 (Upper Permian, Shangshihezi Formation of Jiyuan, Henan Province, China). **A**. IVPP V 4017.5, former *Taihangshania imperfecta* Young, 1979, cervical vertebra in posterior (A_1) and lateral (A_2) views. **B**. HGM 41HIII0427, dorsal vertebra in anterior (B_1) and posterior (B_2) views. **C**, **D**. Sacral vertebrae with ribs. **C**. HGM 41HIII0428, in anterior (C_1) and posterior (C_2) views. **D**. HGM 41HIII0429, in posterior (D_1) and anterior (D_2) views. **E**. IVPP V 4017.27, caudal cervical vertebra in anterior (E_1) and posterior (E_2) views. **F**. HGM 41HIII0430, incomplete right dorsal rib in lateral view.

HGM 41HIII0424, nearly 11 mm in HGM 41HIII0423 (Fig. 1A), but it is more than 14 mm in IVPP V 4016.1 (Fig. 3A) and a newly found tooth.

Compared with the maxillary teeth, the dentary teeth are narrower and taller, being leaf-shaped and with more cusps, similar to *Scutosaurus* and *Shansisaurus* (Lee 2000; Li and Liu 2013) and they are more closely spaced so that some adjacent crowns overlap slightly (Fig. 1E). The dentary teeth are slightly posteriorly inclined with respect to the dorsal margin of the dentary. The posterior three dentary teeth are distinctly smaller than the other teeth. The cusped cingulum is distinct on all but one tooth. The exact number of cusps is hard to count because the cusps merge smoothly into the cusped cingulum, but the number can be estimated as 15. The cusps are regularly spaced along the tooth crown, just as in *Shansisaurus*, *Scutosaurus*, and *Deltavjatia* (Fig. 3D).

The bone surrounding the root extends higher up the crown on the medial than the lateral side, so the tooth seems longer on the lateral than the medial side. This is also observed in other taxa such as *Shansisaurus* (Gao 1983, 1989) and *Deltavjatia vjatkensis* (JL personal observation). In maxillary teeth, the exposed tooth crown is much more than twice the height of the crown above the level of the cingulum, even on the medial side. This is partially because the bone was over-prepared, but the original height of the crown below the level of the cingulum should be greater than the length above. In all other known pareiasaurs, the tooth crown looks much shorter in medial view (Lee 1997b; Jalil and Janvier 2005; Tsuji et al. 2013). Dentary tooth crowns are not as distinct as maxillary crowns.

Two isolated teeth erroneously referred to other groups are identified here as pareiasaur teeth: IVPP V 4018.14, attributed to a gorgonopsian (Young 1979: fig. 12g), and IVPP V 4019.2, attributed to a cynodontian (Young 1979: fig. 13b). IVPP V 4018.14 is a broken tooth with only four cusps preserved (Fig. 3E). It would have had only seven cusps in total, and it is ca. 7 mm in crown width, much smaller than in adults. IVPP V 4019.2 is a tiny tooth that measures 12 mm in height and 2.8 mm in length. Three cusps are closely spaced in the middle, and two cusps lie far below them on two sides. Four cingulum cusps lie between the lower two cusps (Fig. 3F). This tooth is similar to the juvenile teeth of *Scutosaurus* (Lee 1997b: fig.

11MN). These two teeth show that cusp number increases during ontogeny, as has also been observed in *Deltavjatia* (Kordikova and Khlyupin 2001) and *Scutosaurus* (Lee 1997b).

Cervical vertebrae.—Specimen IVPP V 4017.5 (Fig. 4A) was initially identified as a dinocephalian cervical vertebra (Young 1979). It has a large neural canal, amphicoelous centrum, distinct medioventral ridge, well developed diapophysis and parapophysis on the lateral surface of the centrum, mainly anteroposteriorly extending zygapophyses that are narrow mediolaterally, and a slender and tall neural spine that slants anteriorly and expands in mediolateral width dorsally. These features are the same as those of the posterior cervical vertebrae of *Huanghesaurus liulinenesis* (IVPP V 6722; Gao 1983), the probable identity of the present specimen.

Dorsal vertebrae.—Some incomplete dorsal vertebrae are identified from the study material, such as IVPP V 4017.26; but the description is mainly based on the relatively complete specimen HGM 41HIII0427 (Fig. 4B), which is slightly deformed and its centrum and neural spine are broken. The centrum is poorly preserved. The neural arch is wide, swollen, low, massive, and carries a stout neural spine. The zygapophyses are strongly expanded transversely, and their articular surfaces are oval-shape and have radial ripples for the attachment of the musculi interarticulares. The transverse process for articulation with the rib is composed of the fused diapophysis and parapophysis, which is also fused to the process bearing the prezygapophysis. The transverse processes are less wide than the zygapophyses, and the articular surface for the rib is oblique on IVPP V 4017.26. The articular surface for the rib lies at the level of the round neural canal. Both hypantrum and hyposphene are distinct.

Sacral vertebrae.—Two incomplete sacral vertebrae are identified: HGM 41HIII0428 and HGM 41HIII0429 (Fig. 4C, D). Specimen HGM 41HIII0428 is possibly the first sacral, but it is strongly crushed. The sacral ribs are preserved with the centrum, but most of the neural arch and neural spine are lost. The centrum measures approximately 7 cm in diameter and 3 cm in preserved length. Specimen HGM 41HIII0429 is an incomplete vertebra without the centrum and is a posterior sacral. The neural spine is tall, flat and wide; it expands in anteroposterior length upwards. The prezygapophyses are much higher than the postzygapophyses. The width across the prezygapophyses is also much larger than across the postzygapophysis. Both hypantrum and hyposphene are still distinct. The sacral rib is fused to the transverse process.

Caudal vertebrae.—IVPP V 4017.27 (Fig. 4E) was initially identified as a dinocephalian caudal by Young (1979). The anterior surface of the centrum is quite flat and the posterior surface is deeply concave. The neural spine is stout and thins upwards. The poorly developed postzygapophyses ascend to the base of the neural spine. The neural canal is oval. These features indicate it is a pareiasaur caudal.

Rib.—Many incomplete ribs are preserved, and the longest one measures around 40 cm. Most of the ribs are holocephalous, with tuberculum and capitulum connected together, likely dorsal ribs in which the capitulum is broader than the tuberculum (Fig. 4F). Two pairs of sacral ribs are preserved with sacral vertebrae (Fig. 4C, D). The ribs on HGM 41HIII0428 (Fig. 4C) are anchylosed to the centrum, and have an expanded distal portion which is broken. Their proximal width is 11 cm, and the preserved length is 13 cm. The ribs on HGM 41HIII0429 are short (5 cm) and wide (2.5 cm proximally). The distal end is flat and wide (28 mm) and would have reached the ilium.

Scapula.—Specimen HGM 41HIII0431 is a nearly complete right scapula with a height of 42 cm (Fig. 5A). It is a laterally bent bone with a high blade. At the base of the scapular blade, just above the acromion, the bone is very constricted, measuring 8 cm in width. The blade progressively widens dorsally, reaching 14.5 cm in greatest width. The anterior border of the scapular blade is obviously concave, with no trace of a cleithrum while the posterior border is quite straight. The acromion is broken, and its true shape is difficult to determine; but it is broad and thick. It is continuous with the blade and forms the base of its anterior margin. Medial to the acromion is a deep groove that received the lateral end of the clavicle. The glenoid is shallow. Above it, a deep supraglenoid fossa is present, but the supraglenoid buttress and its foramen have disappeared. On the medial side, the subscapular fossa is oval and distinct, but small. In the holotype of *Huanghesaurus liulinensis*, the supraglenoid fossa is indistinct and the subscapular fossa is shallow (Gao 1983).

Interclavicle.—Two differently sized interclavicles were collected, and the larger one (HGM 41HIII0432) is better preserved and is described here (Fig. 5B). This is a robust T-shaped bone, laterally expanded at the transverse bar that curves slightly dorsally. In anterior view, there is an irregular groove on the transverse bar that receives the medial ends of the clavicles. A longitudinal median lamella exists in the groove, showing that there is no fusion between the clavicles. The preserved transverse bar measures 26 cm in width. The bone is elongated downward and backward in a short, wide, median stem. The stem end is slightly expanded and rugose, projecting dorsoposteriorly. As in *Deltavjatia* (Tsuji 2010), a slight ridge extends along the ventral midline of the stem, probably related to the attachment of the pectoralis muscle. The length from the anterior border of the transverse bar to the stem end is 16.5 cm.

Clavicle.—Specimen HGM 41HIII0433 is a slightly damaged left clavicle (Fig. 5C). It is a longitudinally curved strip of bone, relatively thin and blade-like, convex ventrally and concave dorsally. The bone is about the same width for most of its length, tapering slightly at its dorsal and ventral ends. The anterior surface of the bone is convex, except for the concavity at the dorsal and ventral ends. A knob for the omohyoid muscle is developed near the lateral margin on the posterior surface. Ventrally, the clavicle carries a strong keel, which fits in the dorsally facing groove of the interclavicle, while the other part of the posterior surface is excavated for

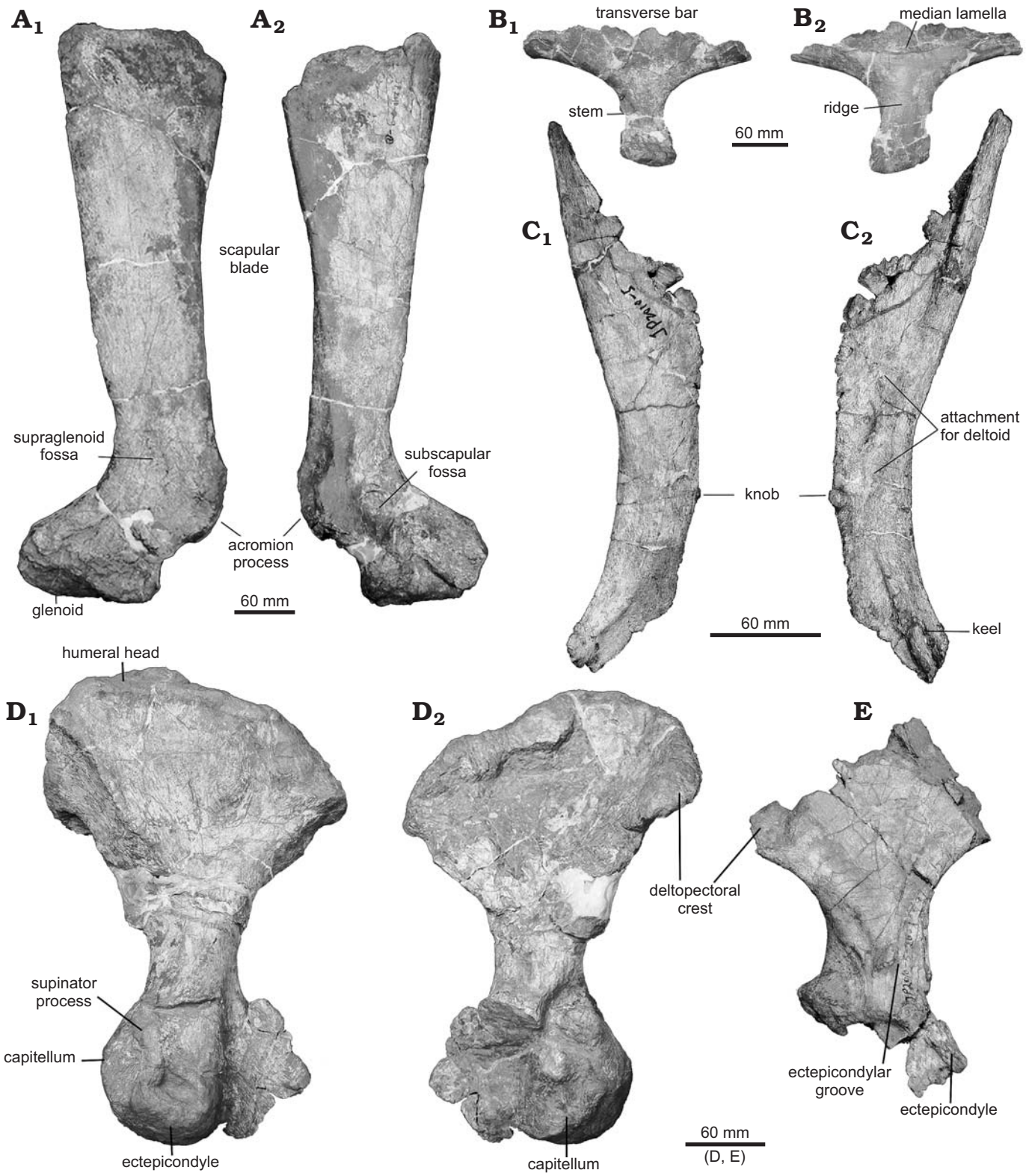


Fig. 5. Pareiasaur reptile *Honania complicidentata* Young, 1979 (Upper Permian, Shangshihezi Formation of Jiyuan, Henan Province, China). **A**. HGM 41HIII0431, right scapula in lateral (A_1) and medial (A_2) views. **B**. HGM 41HIII0432, interclavicle in dorsal (B_1) and ventral (B_2) views. **C**. HGM 41HIII0433, left clavicle in anterior (C_1) and posterior (C_2) views. **D**. HGM 41HIII0435, left humerus in dorsal (D_1) and ventral (D_2) views. **E**. HGM 41HIII0436, right humerus in ventral view.

attachment for the deltoid. The bone curves posterodorsally and laterally, twisting slightly where it is applied to the anterior edge of the scapular blade.

Humerus.—In this locality, four differently sized humeri were collected, suggesting that at least three individuals were buried together. Among them, three are badly broken and

distorted, while the largest one (HGM 41HIII0435) is a relatively complete left humerus with a broken entepicondyle, and the description is based on this specimen and HGM 41HIII0436 (Fig. 5D, E). The humerus is a long, stout bone, with greatly expanded proximal and distal ends, and the shaft is short and cylindrical in cross-section. The proximal and distal expansions are set at around 40° to each other. The largest humerus HGM 41HIII0435 is 33 cm long.

In dorsal view, the proximal surface is divided into two surfaces of different size by an anterior proximodistal line. Anterior and ventral to this line lies the smaller, triangular upper surface of the deltopectoral crest; posterior to this line is a larger, triangular and concave surface. The distal end is expanded by the development of the epicondylar flanges, although the entepicondyle is broken. Proximal to the ectepicondyle is a groove, traversed by the radial nerve and blood vessels. The supinator process is well developed and confluent with the ectepicondyle. No ectepicondylar foramen is observed, although it is universally present in pareiasaurs (Lee 1995, 1997b). The capitulum is well developed but broken and is exposed in dorsal and ventral views.

In ventral view, there is a triangular surface for attachment of the coraco-brachialis on the proximal side of the humerus. The deltopectoral crest extends distally from the anteroproximal corner of the articular surface as a thick edge and thickens to a knob-like surface for the attachment of the pectoralis. Although the entepicondyle is broken, there is an open groove in the position of the entepicondylar foramen (Fig. $5B_2$), the condition also in *Pareiasuchus peringueyi* and *Shihtienfenia permica* (Lee 1997a).

Ulna.—Specimen HGM 41HIII0437 is a right ulna and its proximolateral border is partially broken (Fig. 6A). Its total height, from the tip of the olecranon to the distal end, is 28 cm. The bone is slightly S-shaped in anterior view. Its proximal end, the olecranon, is greatly expanded in width, but is moderately developed in height compared to *Shansisaurus* (Gao 1983). The proximal articular surface is partly bipartite: the larger outer part, which articulates with the humerus, is slightly concave, while the smaller inner part that inclines to the radius side is narrow and flat. Two sigmoid processes under the articular surface of the proximal end are well developed. Between the two processes, is a deep sigmoid notch. The shaft is comparatively thin, but expands again slightly at the distal end. Here, on its medial border, a process is developed which fits against the lateral border of the radius. The articular surface of the distal end is oval and concave.

Radius.—Three distal portions of radii are preserved, and the description is based mainly on IVPP V 4017.20 (Fig. 6B). Compared to the shaft, the distal end is greatly expanded. Its articular surface is roughly triangular and flat, and it is concave when poorly ossified. The posteromedial angle is high and rounded, forming a rounded boss. Along the medial border, a rough area is an area for muscular attachment. In posterior view, there is a shallow groove in the midline for the flexor carpi radialis attachment.

Ilium.—At least four ilia are preserved, and a right one (HGM 41HIII034) is nearly complete but mediolaterally compressed (Fig. 6C). Both ilia underwent different forms of compression during preservation. The ilium has a constricted neck and expanded blade. The iliac blade is laterally concave and smooth. Its anterior margin is long and nearly straight, while the posterior one is short and distinctly concave. Its dorsal margin is convex and the highest place lies on anterodorsal margin. The anterodorsal portion of the iliac blade is rugose and slightly everted. The posterior iliac process is well developed and laterally everted and its dorsal part is also rugose for muscle attachment. The acetabulum is large and rounded, with a prominent supraacetabular buttress. Anterior to the acetabulum, a shallow rugose groove is present. Above the acetabulum, near the anterior border of the shaft, are two rugose stubby crests for attachment of the iliofemoralis. On the medial side, the crista sacralis for connection with the corresponding sacral ribs are developed. The first sacral rib ridge is much more prominent, while the remaining ones diminish posteriorly, suggesting that the first sacral rib is more robust than the rest of the sacral ribs. A round and shallow fossa lies at the position of the fourth crista sacralis, and another shallow fossa lies posteroventral to this. Both fossae could connect to the fourth sacral rib and it is unsure whether there is a fifth sacral rib, although the crista sacralis on the postodorsal corner possibly indicates its presence.

Ischium.—Two pieces of bone (IVPP V 4017.9, 10) could be from same right ischium (Fig. 6D, E). The acetabular and ventral portions are missing. The bone is flat, and the anterodorsal corner is thick, while the thickness diminishes posteriorly and ventrally. A large flange projects dorsolaterally on the posterolateral corner.

Pubis.—Only the proximal end of a right pubis (IVPP V 4017.7) is preserved (Fig. 6F). It is a thick bone with acetabular portion, and the anterior margin extends downwards.

Femur.—Both left and right femora are preserved, and the right femur (HGM 41HIII0439) is fragmentary and distorted, but still more complete (Fig. 7A). It is a broad, massive bone. Both the proximal and distal ends are not obviously expanded. It measures 37 cm from proximal end to distal end, 17 cm in proximal width, and 14 cm in distal width. The femoral head is broken. The capitellum on its proximal end is a flat area and does not extend onto the dorsal surface. The trochanter major, which is located away from the proximal end on its posterior border, is well developed, but its posterior flange is broken. The postaxial flange runs the entire length of the femur, and the femur appears extremely wide with the postaxial border appearing as a straight edge. A remarkable feature of the dorsodistal end is the presence of a prominent, stout process, which starts from the distal end along the midline, but decreases until the middle part of the shaft. Along the posterior margin of the lateral condyle is a groove for reception of the proximal end of the fibula. The dorsal border of the groove is formed by a distinct tubercle, which projects posteriorly. Ventrally, the internal trochanter is long, but the

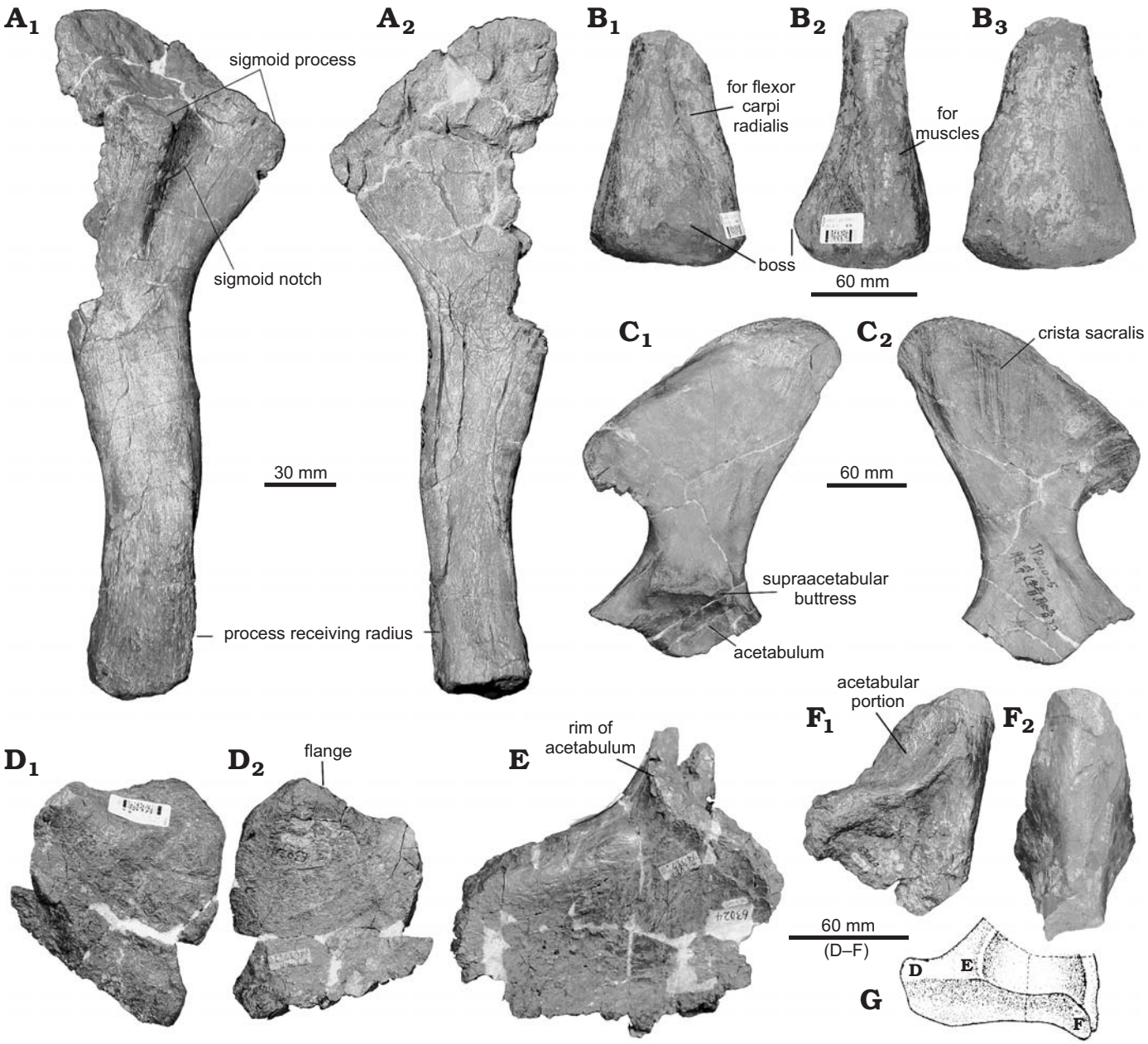
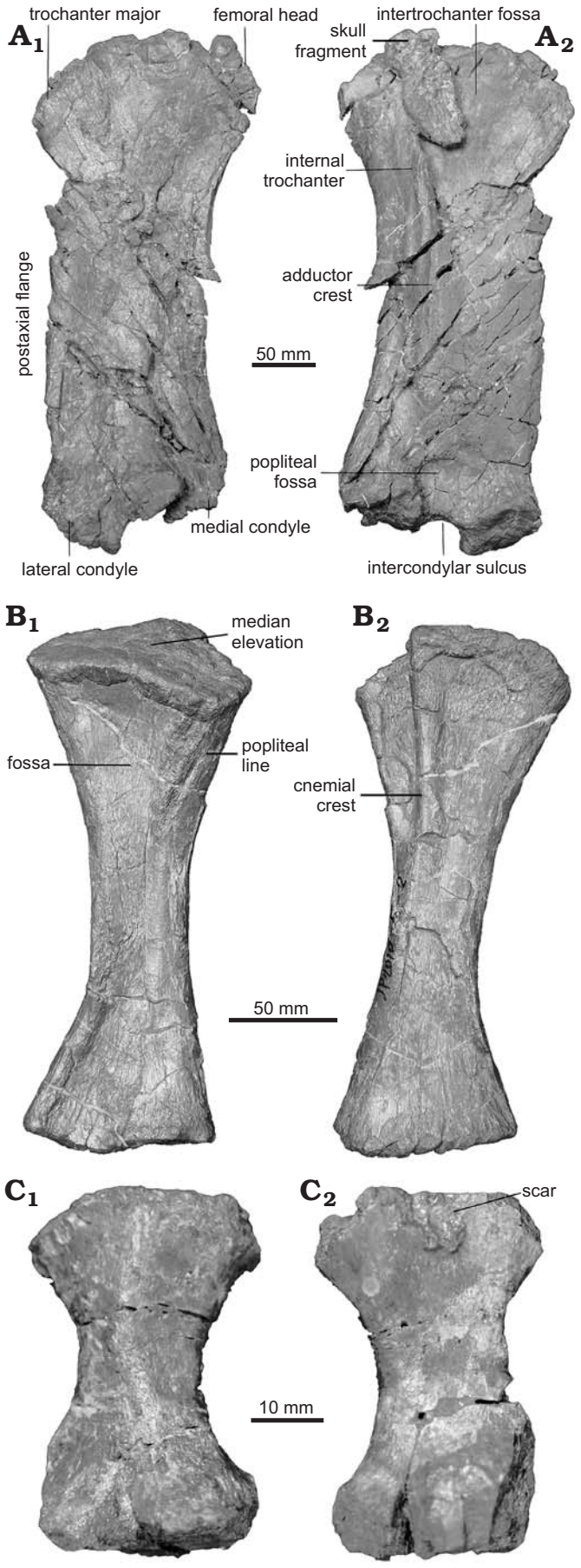


Fig. 6. Pareiasaur reptile *Honania complicidentata* Young, 1979 (Upper Permian, Shangshihezi Formation of Jiyuan, Henan Province, China). **A**. HGM 41HIII0437, right ulna in anterior (A_1) and posterior (A_2) views. **B**. IVPP V 4017.20, distal end of left radius in posterior (B_1), medial (B_2), and anterior (B_3) views. **C**. HGM 41HIII0434, right ilium in lateral (C_1) and medial (C_2) views. **D**. IVPP V 4017.10, distal part of right ischium in medial (D_1) and lateral (D_2) views. **E**. IVPP V 4017.9, partial right ischium in lateral view. **F**. IVPP V 4017.7, proximal part of right pubis in lateral (F_1) and anterior (F_2) views. D–F were referred to *Taihangshania imperfect* in Young 1979. **G**. Pelvic girdle reconstruction showing the position of D–F.

proximal region is curved, so the anterior side is concave and the posterior side convex. Distal to the internal trochanter, a stout adductor crest is present for attachment of the adductor femoris. It extends medially from the proximal end, but diminishes before reaching the distal end. Posterior to the adductor crest is a large intertrochanteric fossa for insertion of the puboischiofemoralis. The popliteal fossa is a rounded, shallow depression on the surface between entepicondyle and ectepicondyle. The two condyles are separated by a deep, rounded intercondylar sulcus. The surfaces of the two condyles are rugose, project ventrally and both receive the tibia.

A bone fragment associated with the femur could be part of the posterior margin of the skull.

Tibia.—A right tibia (HGM 41HIII0440) is well preserved, but slightly deformed (Fig. 7B). It is 24 cm long. The tibia is expanded at both proximal and distal ends, but the shaft is relatively constricted. Both proximal and distal articular surfaces are rough, indicating that they were covered by cartilage. The proximal articular surface has a median elevation, which probably fitted between the two lateral condyles of the femur. On the anterior side, below the proximal end, the prominent cnemial crest extends longitudinally downwards to



the middle of the shaft. Lateral to the cnemial crest, is a deep concave groove for reception of the fibula. On the posterior surface, the popliteal line extends downwards and medially, forming a narrow triangular fossa with the medial margin.

Metapodial.—Specimen HGM 41HIII0443 is identified as either a metacarpal or metatarsal (Fig. 7C). The proximal end is broken but thick. The distal end is compressed, with a slightly concave ventral surface and convex dorsal surface, while its distal articular surface is concave. A small scar is present on the ventral surface, indicating a place for muscle attachment.

Discussion

The new material confirms the proposal of Lee (1997a) that *Tsiyuania* and *Honania* represent the upper and lower jaw teeth respectively. Lee (1997a) also recognized the similarity of the maxillary teeth from Jiyuan (*Tsiyuania*) with those of *Sanchuansaurus*, so he referred the dentary teeth from Jiyuan (*Honania*) to *Sanchuansaurus* too, although the dentary teeth of *Sanchuansaurus* were unknown. Our recent work has showed that *Sanchuansaurus*, *Huanghesaurus*, and *Shansisaurus* are synonymous and the dentary teeth of *Sanchuansaurus* are indeed the same as the teeth of the holotype of *Huanghesaurus* (Li and Liu 2013). However, the dentary teeth from Jiyuan are quite different from those of *Huanghesaurus* in that the lingual surface of the crown is smooth in *Honania* but bears a distinct triangular ridge in *Huanghesaurus*. The new cranial material shows even more differences between the two taxa: the similar maxillary teeth are less closely spaced in *Honania* than in *Huanghesaurus*; the maxillary boss is more robust and with a knob in *Shansisaurus* but is moderately developed in *Honania*; almost all dentary teeth have a cusped cingulum in *Honania*, while only a few dentary teeth have a less obvious cusped cingulum in *Huanghesaurus*; the posterior margin of the scapula is straight in *Honania*, but concave in *Huanghesaurus* and *Shitienfenia* (Young and Yeh 1963; Cheng 1980; Gao 1983), the subscapular fossa is large and deep in *Honania* but small and shallow in *Huanghesaurus* and *Shitienfenia*; the humerus is less expanded in *Honania* than in *Huanghesaurus* and *Shitienfenia*; an entepicondylar foramen is absent in *Honania*, but present in *Huanghesaurus*; the ulnar olecranon is moderately developed in *Honania*, but well developed in *Huanghesaurus*; the iliac dorsal margin is slightly convex in *Honania*, but slightly concave in *Shitienfenia*.

Almost all marginal teeth have a cusped cingulum in known pareiasaur specimens from Jiyuan; this character could

Fig. 7. Pareiasaur reptile *Honania complicidentata* Young, 1979 (Upper Permian, Shangshihezi Formation of Jiyuan, Henan Province, China). **A**. HGM 41HIII0439, right femur in dorsal (A_1) and ventral (A_2) views. **B**. HGM 41HIII0440, right tibia in posterior (B_1) and anterior (B_2) views. **C**. HGM 41HIII0443, metatarsal or metacarpal in anterior (C_1) and posterior (C_2) views.

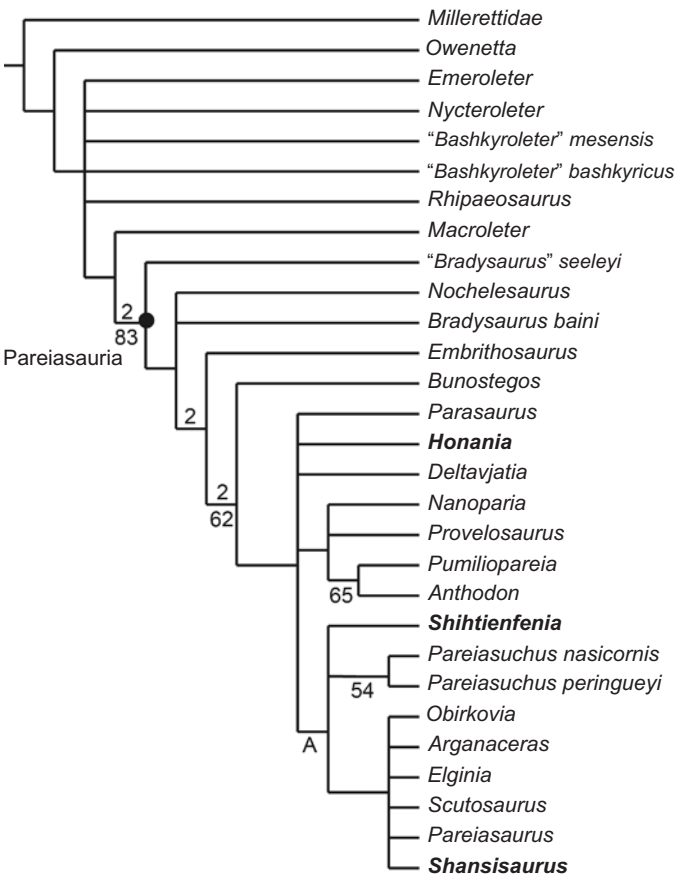


Fig. 8. Cladistic relationships of *Honania complicidentata* within Pareiasauria. A strict consensus of most parsimonious topologies recovered from TNT analyses (90 trees under traditional search, 6 trees under new technology search). Bremer decay values above one and bootstrap values >50% are listed above and below, respectively, each well-supported branch.

be unique among pareiasaurs. The cingulum is not cusped in *Parasaurus* (Tsuji and Müller 2008). Only some teeth that are randomly distributed in the jaws have a cusped cingulum in *Scutosaurus* (Ivachnenko 1987; Lee 1997b), and *Deltavjatia* (Tsuji 2013). The cusped cingulum is present on the maxillary teeth of *Arganaceras* and *Shansisaurus* and a few dentary teeth of *Shansisaurus* (Gao 1989; Jalil and Janvier 2005; Li and Liu 2013), while the dentary teeth of *Arganaceras* are unknown. Even if all marginal teeth have a cusped cingulum in *Arganaceras*, the Jiyuan specimens are differentiated by the ventrally directed maxillary teeth, which are anteroventrally directed in *Arganaceras*. Based on only dental characters, we show that the Jiyuan pareiasaur material represents a valid taxon, and the name *Honania complicidentata* is reestablished here, while *Tsiyuania simplicidentata* and *Taihangshania imperfacta* are its junior synonyms. In *Honania*, the height of the exposed tooth crown is much greater than twice the height of the crown above the level of the cingulum, and the dentary teeth are slightly posteriorly inclined compared to the dorsal margin of the dentary. These two characters are also autapomorphies of this taxon.

To test the phylogenetic position of *Honania complicidentata*, we put this taxon in the recent data matrix of Tsuji et al. (2013), and *Sanchuansaurus* is excluded and *Shansisaurus* is included because the former is a junior synonym of the latter (Li and Liu 2013). Two characters are modified, some codings are revised and *Honania complicidentata* is coded in this matrix (Appendix 1 and Supplementary Online Material available at http://app.pan.pl/SOM/app60-Xu_etal_SOM.pdf). The new matrix was searched using traditional search with 5000 random addition sequences and 1000 trees per replication using the Tree Bisection Reconnection (TBR) algorithm and using New Technology Search in TNT (Goloboff et al. 2008), Millerettidae was the only outgroup. Although the number of minimum length trees (219 steps) is different in both cases, the strict consensus trees are same and are very similar to the result of Tsuji et al. (2013: fig. 10): the position of *Shansisaurus* is the same as the previous position of *Sanchuansaurus*, the position of *Shihtienfenia* is similar, but the positions of *Parasaurus* and *Deltavjatia* are changed (Fig. 8). The position of *Honania* is unresolved: it could be the sister-group of Velosauria plus *Parasaurus*, or the sister-group of Group A on Fig. 8, but it is always more basal than *Shansisaurus* and *Shihtienfenia* from the Sunjiagou Formation. However, these phylogenetic results are unstable and they could be changed when more characters are coded in the matrix.

Conclusions

The pareiasaur specimens from Jiyuan represent a valid taxon, and the name *Honania complicidentata* is reestablished. *H. complicidentata* is characterized by maxillary teeth with high crowns, dentary teeth slightly posteriorly inclined compared to the dentary dorsal margin, nearly all preserved marginal teeth have a cusped cingulum on the lingual surface, and humerus without an ectepicondylar foramen. *Honania* is more basal than *Shansisaurus* and *Shihtienfenia* from the Sunjiagou Formation.

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Appendix 1

Modifications to character list and data matrix of Tsuji et al. (2013).

Redefined characters:

(51) Number of maxillary teeth in each maxilla: more than or equal to 20 (0); less than or equal to 18 (1). [Codings are not changed for this character]

(57) Cusped cingulum on the lingual surface of the marginal teeth: absent (0); only on some teeth (1); on almost all maxillary teeth at least (1). [Codings were changed for three taxa: *Parasaurus* 0 *Arganceras*, and *Shansisaurus* 2]

Shansisaurus	?????????? ?????????? ??1?01???? ?????????? ?????1??10 11[01]3412???? ??????1211 111?00???? 0????????? ???1?1??? ?????????? ????????1? ????0??
Honania	?????????? ?????????? ??1?00???? ?????????1 ?????1???0 ?1[01]3402???? ?[23]????12?11 1??100???0 ??1111110? ??11210??? 1????????? ??????1??? ??0??